

Fruit-feeding in European cold season noctuid moths increases fecundity, but not longevity

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Abstract. Feeding on rotting fruits, rather than nectar, is linked to high adult life-expectancy in certain butterflies, notably tropical Nymphalidae. We experimentally tested whether cold-season central European noctuid moths may also derive longevity and fecundity benefits from feeding on fruits. Many cold-season noctuid moths avidly feed on such resources. We expected fitness benefits to be especially pronounced in moths which overwinter as adults, in relation to their unusually long and thus nutrient-demanding imaginal life (6–9 months). Field-caught female individuals representing four genera (*Allophyas* Tams, 1942; *Agrochola* Hübner, 1821; *Conistra* Hübner, 1821; *Eupsilia* Hübner, 1821) were offered sucrose solution, sucrose solution enriched with vitamins, or moisturized banana slices plus sucrose solution, respectively, under greenhouse conditions. These moths represented two life-cycle types (autumn species vs. adult hibernators). Life span differed between moth genera, but we did not observe any enhancement of life span through fruit-feeding. Rather, in some cases moths kept with access to banana slices experienced a minor reduction in life span, compared to moths fed sucrose solution only. We observed no benefits in terms of enhanced fecundity through fruit-feeding in autumn species. Among adult hibernators, in contrast, potential fecundity increased by over 50% in banana-fed females, when observed over their full lifetime. Yet, if kept in the lab only after completing their hibernation in the wild, fitness benefits no longer accrued to moths from supplementing their diet with fruits. We conclude that noctuids that hibernate as adults are indeed income breeders which potentially increase their fecundity by feeding on fruits.

Introduction

Regarding the sources of their reproductive investment, adult lepidopterans span the full range from capital to income breeders (Holm et al. 2016). While capital breeders derive all energy required during their adult stage from resources accumulated as larvae, in income breeders reproductive success also depends on nutrient intake of the imago. Carbohydrates and, more rarely so, amino acids taken up with nutritious liquids have been shown to increase longevity or fecundity in a range of butterfly and moth species (Bauerfeind and Fischer 2005; Mevi-Schütz and Erhardt 2005; Cahenzli and Erhardt 2012, 2013). Supplementing nectar carbohydrates with amino acids from pollen results in life-expectancies of 6–9 active months, but is confined to a small fraction of Neotropical *Heliconius* Kluk, 1780 butterfly species (Gilbert 1972; O'Brien et al. 2003). Tropical butterflies which feed on rotting fruit rather than floral nectar may achieve substantial fitness benefits from that mode of resource specialization (Bauerfeind and Fischer 2005; Beck 2007). Overall, fruit feeding in butterflies seems to be strongly linked to high longevity, with some tropical nymphalid butterflies (e.g. *Euphaedra medon* (Linnaeus, 1763)) surviving up to 293 days as adults without dormancy (Molleman et al. 2007).

We here set out to experimentally investigate whether fitness benefits in terms of life-expectancy or fecundity also accrue to moths which feed on rotting fruits. In Europe, few moth species are specialist fruit feeders, but many opportunistically utilize such resources whenever available (Ebert 1997–1998; Süßenbach and Fiedler 1999). In central Europe, the habit of feeding on rotting fruits is especially prevalent amongst Noctuidae species whose adult flight period covers the cold season, i.e. when floral nectar resources are scarce or totally lacking. The strong attraction to rotting fruits might even indicate that moth species using this type of resource gain fitness advantages over mere nectar feeding. Such benefits could be rooted in a more balanced complement of nutrients in fruits as opposed to nectar. In particular, fruits are expected to contain more vitamins or micro-nutrients than standard floral nectars that are notoriously dominated by a few mono- and disaccharides as nutrient compounds (González-Teuber and Heil 2009; Heil 2011).

From a bionomics perspective, central European cold season noctuid species can be divided into autumn species and adult hibernators. Autumn species emerge from the pupa between late August and October. They soon mate and lay their eggs until the onset of true winter weather (usually in November) when all adults die and only the eggs overwinter. Typical representatives are genera such as *Agrochola* Hübner, 1821 and *Allophyes* Tams, 1942. Adult hibernators (like *Eupsilia* Hübner, 1821 and *Conistra* Hübner, 1821) also emerge in autumn, but mating and egg-laying only take place in early spring, after hibernation. These moths intermittently resume flight activity during spells of mild weather in winter when remnants of rotting fruits may provide the only potential food resource. Adults of these hibernator species survive through to April or May, i.e. have life-expectancies of 6–9 months.

We sampled representatives of both life-cycle types from wild populations and subjected them to a feeding experiment in the laboratory. Specifically, we tested two hypotheses:

- (a) When given access to a fruit resource of standardized quality in addition to pure carbohydrates, cold season noctuid moths survive for longer periods and lay more eggs than individuals offered sucrose solution only.
- (b) Fitness benefits are more pronounced in noctuid species overwintering as adults which thus must survive longer, whereas benefits are smaller in more short-lived autumn species.

Material and methods

Moth sampling

Most moths were attracted using a bait mixture of red wine and sucrose (1:1 weight relation; e.g. Süßenbach and Fiedler 1999). Pieces of cotton cloth (approx. 5 × 10 cm in size) were soaked with this bait and exposed 1.3–1.7 m above ground on shrubs or trees at forest edges. Some additional moths used for experiments were attracted to a light tower (a gauze tower, 1.6 m high, diameter 0.7 m, equipped with two 15 W tubes: F15W/350BL-T8 UVA & F15W/BL B-T8, Sylvania). We sampled moths in the Nationalpark Donau-Auen, about 20 km east of Vienna, Austria (48°08'N, 16°41'E). The region is known to harbour a species-rich moth fauna typical for Central European lowland floodplain forests (Truxa and Fiedler 2012, 2016). There were 27 sampling evenings in the period from 25.ix.–15.xi.2005, and 6 evenings from 30.iii.–9.iv.2006. We exposed baits around sunset, and moths were taken at the baits over a period of 3–4 h per evening. Sampling only took place when ambient temperature was above 0 °C and there was no rain. Altogether, the following numbers of female moths entered into the experiments: 71 *Allophyes oxyacanthae* (Linnaeus, 1758); 14 *Agrochola circellaris* (Hufnagel, 1766); 3 *Agrochola macilenta* (Hübner, 1808); 63 *Eu-*

psilia transversa (Hufnagel, 1766); 76 *Conistra vaccinii* (Linnaeus, 1761); 6 *Conistra rubiginosa* (Scopoli, 1763); 1 *Conistra rubiginea* ([Denis & Schiffermüller], 1775); and 3 *Conistra erythrocephala* ([Denis & Schiffermüller], 1775).

Treatment in captivity

Upon capture, moths were put in glass vials (50 ml, lined with a piece of filter paper, with air holes in the lid), transferred into a cool and dark bag, kept in a refrigerator overnight and on the next day transported into the laboratory. On the morning after capture, each moth was identified to species and placed into an individually marked rearing jar (transparent 500 ml plastic cups covered with gauze on top). The bottom of each jar was lined with moist filter paper to maintain sufficient humidity. All moths had access to water ad libitum and to cut twigs of their larval host plants for egg laying. Jars were positioned in a greenhouse on the roof of the university building. Temperature varied substantially, with average temperature during day-time being 18 °C (maximum: 26 °C) and 12 °C (minimum: 7 °C) during the nights.

Moths were randomly assigned to one of three feeding treatments: (1) sucrose solution (150 g sucrose in 1000 ml distilled water); (2) sucrose solution of the same concentration, enriched with 7.5 g vitamin mixture (Vanderzant vitamin mix for insects no. 300100, Dyets Inc.; for composition see: <http://dyets.com/vitamin-mixes>); and (3) the same sucrose solution as in treatment (1) supplemented with fresh slices of banana. A 15 % sugar content (wet weight) in a nectar mimic is rather at the lower edge of profitability for nectarivorous Lepidoptera (e.g. May 1988; Rusterholz and Erhardt 1998) so that beneficial effects of supplementary nutrients could be expected to be particularly strong. Nutrient solutions were offered in 1 ml tubes, while banana slices were placed on top of the gauze lids. Banana was chosen since this fruit can be obtained in standardized quality throughout the year. Fruit slices were kept moist by spraying them with water daily. Sucrose solutions and banana slices were replaced every 2–6 days, as required. For analyses we only considered female individuals. We attempted to achieve a roughly even distribution of individuals across the three food treatments and life-cycle types.

Data collection and statistical analysis

Moths were inspected every 1–2 days, and it was noted if they were still alive. All eggs they had laid were removed and counted. Every individual was followed until its death. Dead moths were preserved in 70% ethanol and later dissected under a stereo microscope. Upon dissection, the number of mature oocytes was counted. The length of time between date of capture and death in captivity was taken as measure of the moth's physiological life span. We used the sum of eggs laid in captivity plus the mature oocytes remaining in the abdomen after death as a measure of potential fecundity. Longevity and fecundity data were log-transformed to improve fit to normality and homoscedasticity assumptions.

For analysis, we partitioned our data into three subsets: (1) autumn species; (2) adult hibernators that remained in the experiment throughout winter; and (3) adult hibernators that had only been collected in early spring, after hibernation in the wild. Autumn moths comprised representatives of two genera (*Allophyes* and *Agrochola*). Adult hibernators were *Eupsilia transversa* and representatives of the genus *Conistra*. We analysed our data by means of Gaussian Linear Models (GLMs), with food treatment and moth genus as categorical predictors. Capture date was included as a covariate to account for the fact that individuals sampled later in their flight season had spent some (unknown) fraction of their life span before being caught for the experiment. For the analysis of fecundity data, we included time spent in the lab as covariate, to account for its potential influence on the number of eggs produced during the

experiment. GLMs for longevity and fecundity were run separately for each of the three data partitions outlined above. Inspection of residuals revealed excellent fit of model assumptions in every case. Throughout the text, means of untransformed data are reported, together with their standard errors, for ease of comprehension. Analyses were performed with Statistica 8.0 (StatSoft Inc.).

Results

Longevity

In autumn moths, capture date had a clear effect on life-expectancy: the later individuals were caught in the season (standardized regression coefficient: $\beta = -0.255 \pm 0.081$), the shorter was their remaining life in captivity. *Allophyes oxyacanthae* were far more short-lived (11.0 ± 0.4 d; maximum: 21 d) than *Agrochola* moths (27.3 ± 4.6 d; maximum: 69 d; Table 1). Moths kept with access to banana slices in addition to sucrose solution lived a significantly shorter time than those in the two other food treatments, but this effect was confined to *Agrochola* moths, as indicated by the significant genus \times food interaction term (Fig. 1a).

In adult hibernators overwintering in the lab, capture date was only weakly and not significantly associated with remaining life span ($\beta = -0.080 \pm 0.192$). *Eupsilia transversa* were not significantly more long-lived (135.4 ± 4.8 d; maximum: 156 d) than *Conistra* moths (128.9 ± 10.2 d; maximum 198 d), and adult food type had no significant influence on longevity (Table 1; Fig. 1b).

Finally, among adult hibernators that had overwintered in the wild, capture date was again strongly and negatively associated with remaining life span ($\beta = -0.275 \pm 0.095$). *Eupsilia transversa* females survived for almost the same period of time in the lab (19.1 ± 0.8 d; maximum: 32 d) as did *Conistra* moths (18.1 ± 0.5 d; maximum: 28 d). Adult food type significantly influenced

Table 1. Results of GLMs (*F* statistics and *p* values) on moth longevity (log-transformed), with genus and experimental food treatment as categorical factors, and date of capture as covariate. In the two adult hibernator genera, analyses were further partitioned between individuals that had hibernated in the lab, or were included into the experiment only after natural hibernation. df – degrees of freedom. Significant results (*p*<0.05) printed in bold. See Fig. 1 for means and confidence intervals.

	df	<i>F</i>	<i>p</i>
Autumn species			
Genus	1	40.97	<0.0001
Food type	2	4.54	0.0135
Genus \times Food type	2	4.18	0.0186
Capture date	1	9.94	0.0023
Residual	82		
Adult hibernators, lab			
Genus	1	0.85	0.3627
Food type	2	0.23	0.7957
Genus \times Food type	2	0.08	0.9231
Capture date	1	0.18	0.6779
Residual	30		
Adult hibernators, field			
Genus	1	0.01	0.9286
Food type	2	3.69	0.0284
Genus \times Food type	2	0.49	0.6142
Capture date	1	8.32	0.0048
Residual	105		

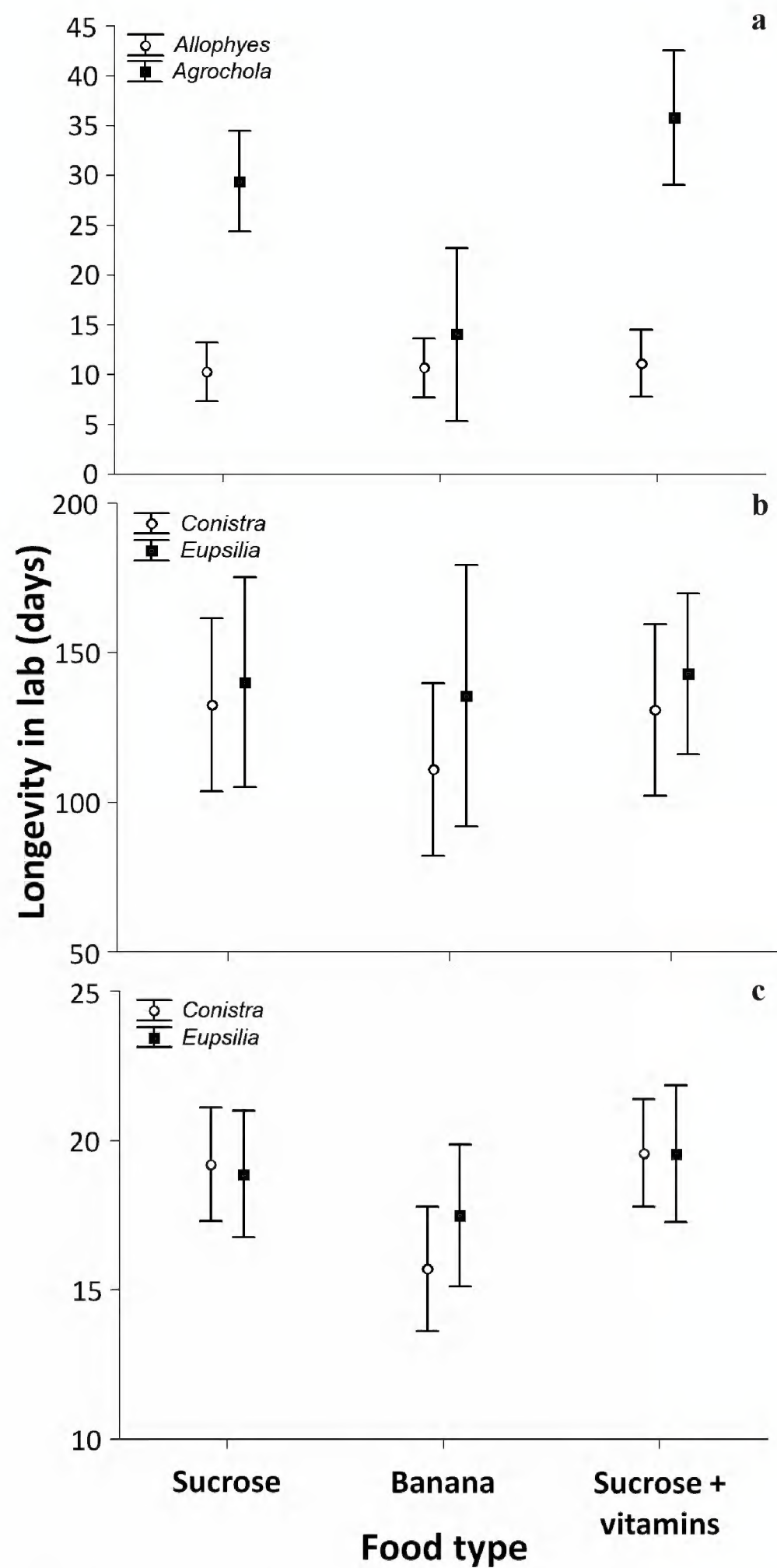


Figure 1. Longevity of cold season noctuid moth females in captivity, according to the three experimental food treatments. ‘Banana’ refers to moths that had access to fruit slices in addition to sucrose solution as adult food. Given are means (controlling for capture date) and 95% confidence intervals. **a** autumn moths **b** adult hibernators captured in autumn and overwintered in the lab **c** adult hibernators captured after hibernation in the wild.

longevity, with moths offered access to banana slices having lower average life spans after hibernation than those fed only sucrose, or sucrose plus vitamins, solution.

Potential fecundity. Among autumn moths, *A. oxyacanthae* had less than half of the reproductive potential (180.2 ± 10.6 eggs; maximum: 429) than that seen in *Agrochola* females (528.8 ± 54.3 eggs; maximum: 848; Fig. 2a). The longer moths survived in captivity, the more eggs they produced ($\beta = 0.531 \pm 0.091$). However, adult food did not modulate reproductive capacity, nor was there a differential response to food type between the two moth genera (Table 2). Inspection of their bursa copulatrix revealed that all these moths had been mated prior to collection, apart from four *A. oxyacanthae* individuals and two *Agrochola macilenta*. Overall, potential fecundity in the adult hibernator species was far higher. When hibernated in the lab, *Conistra* (730.4 ± 55.3 eggs; maximum: 1100) and *Eupsilia* (604.9 ± 79.5 eggs; maximum: 1427) had similar reproductive capacity, and their life span in the lab was not significantly associated with potential fecundity ($\beta = 0.1023 \pm 0.1495$). However, there was a strong effect of adult food: moths kept with access to banana slices in addition to sucrose solution produced on average over 50% more eggs or oocytes (985.9 ± 78.9) than those in the other two food treatments (with mean fecundity around 600 eggs; Fig. 2b). Except one *Eupsilia* female, none of these moths had been mated when entering into the experiment. When moths of the same life-cycle type were transferred to the lab only after hibernation in the wild, the pattern changed distinctly. Then, *Eupsilia* moths produced far more eggs (853.1 ± 41.7 eggs; maximum: 1569) than *Conistra* females (476.8 ± 17.6 eggs, maximum: 1141) and potential fecundity was again strongly and positively associated with life span in the lab ($\beta = 0.3040 \pm 0.0686$). However, access to banana slices supplementing the sucrose nectar mimic no longer had any detectable influence on fecundity (Table 2, Fig. 2c). All of the females that had hibernated in the wild were mated at the time of capture.

Table 2. Results of GLMs (*F* statistics and *p* values) on moth fecundity (log-transformed), with experimental food treatment and moth genus as categorical factors, and life-time in the lab (log-transformed) as covariate. Among adult hibernators analyses were further partitioned between individuals that had hibernated in the lab, or were included into the experiment only after natural hibernation. df – degrees of freedom. Significant results (*p*<0.05) printed in bold. See Fig. 2 for means and confidence intervals.

	df	<i>F</i>	<i>p</i>
Autumn species			
Genus	1	11.71	0.0010
Food type	2	1.88	0.1599
Genus × Food type	2	0.46	0.6317
Longevity	1	33.91	<0.0001
Residual	81		
Adult hibernators, lab			
Genus	1	0.25	0.6217
Food type	2	5.02	0.0134
Genus × Food type	2	2.90	0.0711
Longevity	1	0.47	0.4991
Residual	29		
Adult hibernators, field			
Genus	1	89.76	<0.0001
Food type	2	0.96	0.3878
Genus × Food type	2	2.39	0.0967
Longevity	1	19.64	<0.0001
Residual	104		

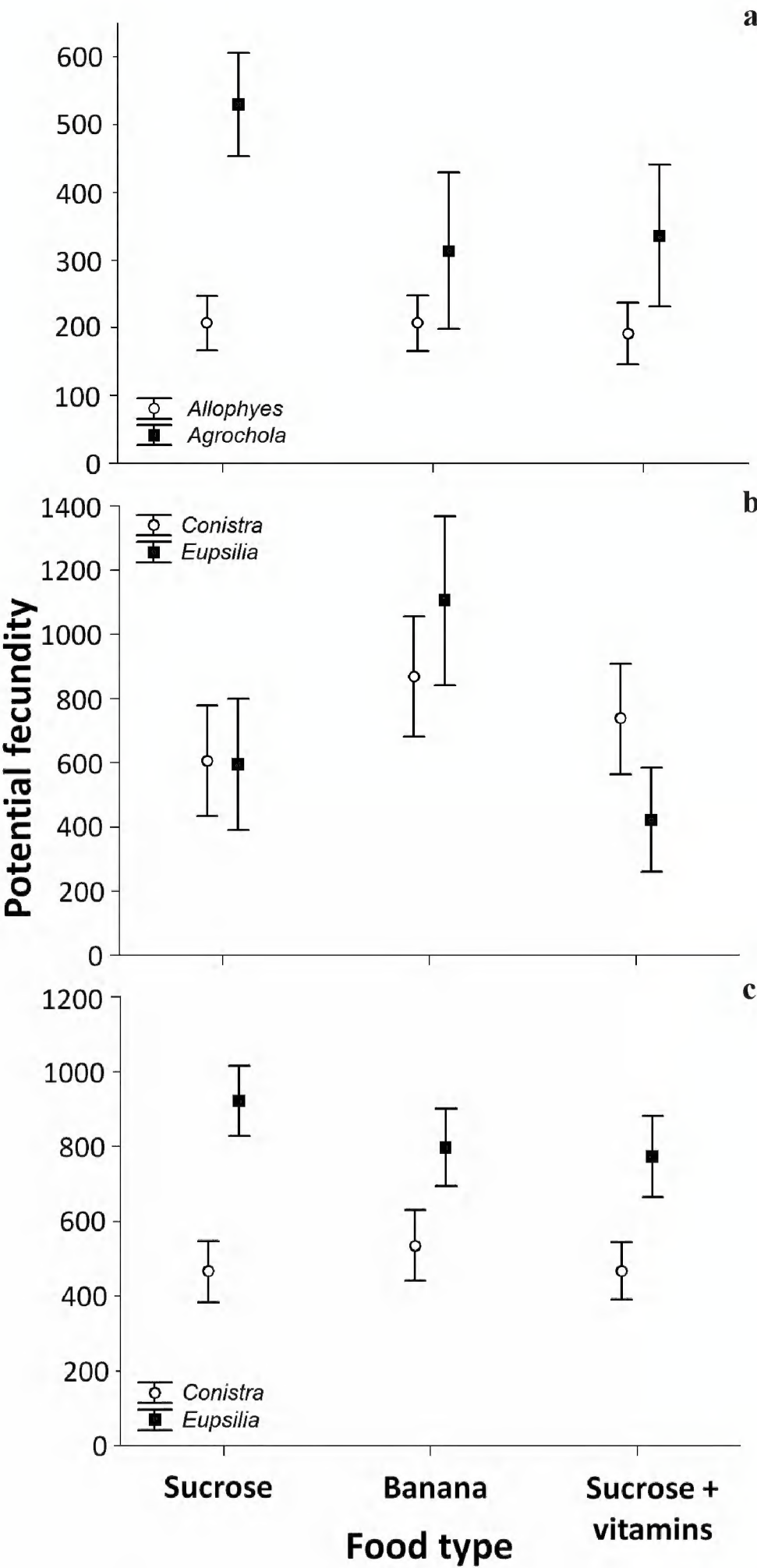


Figure 2. Potential fecundity of cold season noctuid moths in captivity, according to the three experimental food treatments. ‘Banana’ refers to moths that had access to fruit slices in addition to sucrose solution as adult food. Given are means (controlling for life expectancy in the lab) and 95% confidence intervals. **a** autumn moths **b** adult hibernators captured in autumn and overwintered in the lab **c** adult hibernators captured after hibernation in the wild.

Discussion

Fitness benefits. Concerning moth longevity our experiments revealed no benefits from feeding on fruits, relative to solely sucrose-feeding. This result was comparable across four genera of Central European cold season noctuid moths representing two different life-cycle types (adults only active in autumn; or adults active from autumn to spring with imaginal dormancy). In fact, where subtle food effects could be observed at all, these were in the opposite direction than what might have been expected: female *Agrochola* and *Conistra* kept with access to banana slices in addition to sucrose solution even lived slightly shorter in the laboratory than pure sucrose feeders. Enrichment of the nectar mimic with a vitamin mixture had no discernible effect on life span in any of the three experimental groups.

These results are surprising at a first glance, since other studies have established a clear link between longevity and fruit-feeding in butterflies (Molleman et al. 2007; Bauerfeind and Fischer 2005). Also in multi-species comparisons, the habit of feeding on rotting fruits was associated with unusually long adult life-spans (Molleman et al. 2007; Beck 2007; Beck and Fiedler 2009). Yet, such statistical contingencies across species do not necessarily indicate a causal relationship between high life-expectancy and fruit feeding within species.

Rather, our findings challenge the notion that fruit-feeding among adult Lepidoptera were per se associated with high longevity. This relationship appears to hold true for specialist fruit-feeders like the African satyrine butterfly *Bicyclus anynana* (Butler, 1879) (Bauerfeind et al. 2007; but see Molleman et al. 2008), and many other tropical genuine fruit-feeders. Here fruit-feeding as a specialist strategy has been selected for in combination with a suite of other life-history characters. In contrast, for nectarivores among the Lepidoptera which only visit fruits to opportunistically supplement their diet when needed, this resource use does not necessarily yield longevity benefits over the mere use of nectar.

We attribute this lack of positive response to the digestive physiology of essentially nectarivorous moths. Licking at banana slices will likely yield dissolved mono- and disaccharides as well as other dissolved micro-nutrients. Yet, these nutrients did apparently not translate into longevity benefits. Moreover, fruit slices undergo microbial decay under the relatively warm and humid conditions in our experiment (E.-M. McMannis and K. Fiedler, unpublished observations). Even though we replaced fruit slices frequently this decay may have been the reason for premature death in some banana-fed individuals, especially in *Agrochola* and *Conistra* moths.

In insects that specialize on rotting fruits, decomposition products, such as yeast amino acids, and the complex admixture of nutrients encountered in fruits are essential to achieve fitness benefits (Bauerfeind et al. 2007; Geister et al. 2008; Molleman et al. 2008; Beaulieu et al. 2017). To better locate their resources, specialist fruit-feeders also tend to be highly responsive to alcohols and other by-products of microbial decay of fruits (Ômura et al. 2000; Dierks and Fischer 2008; Tang et al. 2013). While noctuid moths may be responsive to complex odour blends emitted by food resources (e.g. Gregg et al. 2010), we are unaware of any studies on the perception of rotting fruit volatiles among these insects.

While we did not observe any increase of life span through access to fruit in addition to sucrose, clear positive effects of fruit-feeding on moth fecundity could be established. However, this increase in potential fecundity was confined to the two genera *Eupsilia* and *Conistra*. These unusually long-lived moths hibernate as adults and thus experience particularly strong demands for nutrient income beyond their larval stages. Indeed, benefits were very substantial, with an increase in potential fecundity of >50% as compared to individuals kept on an exclusive carbohydrate diet. These considerable

fitness benefits however, only became apparent in moths captured in autumn and subjected to the experiment over the whole winter into early spring, i.e. over a life time of 3–4, and occasionally more than 5, months. In representatives of the same moth species subjected to the food treatments just after hibernation in the wild, the beneficial effects of banana feeding totally vanished. We attribute this to the rather short remaining life span of these insects after hibernation (on average about 2.5 weeks in the laboratory). This time was probably insufficient to allow these insects to gain additional advantages in terms of egg maturation, beyond the fitness benefits accruing from sugar consumption alone. In line with this interpretation, we did not observe any fecundity benefits from providing banana slices in addition to carbohydrates in the autumn moths with their average adult life-span of just 2–3 weeks.

Except for one single *Eupsilia transversa* female, none of the adult hibernators sampled in autumn had already been mated when entering into the experiment. Hence, these moths lacked all nutrients they might possibly derive from the spermatophore donated by their mates (Torres-Vila et al. 2004). In contrast, all *Conistra* and *Eupsilia* females captured in early spring were mated when transferred into the laboratory. It is possible that the absence of spermatophores increased the fecundity effect of additional nutrients in the lab-hibernated females.

All moths studied in our experiment are opportunistic feeders during their adult stage. They drink floral nectar whenever available (see Ebert 1997–1998 for records of flower visits of our study species in SW Germany). Apparently, concentrated sucrose solution provides these moths with sufficient nutrients relevant to longevity and fecundity, except for those few species with extraordinarily long adult life-spans. Hence, the habit of avidly feeding on rotting fruits as seen in these cold-season moths does not offer them a genuine advantage over nectar feeding. Rather, our results suggest that this peculiar habit just helps cold-season moths to survive periods of very restricted availability of nectar flowers.

Differences between taxa in life-history strategies. The principal aim of our experimental study was to compare the two life-history types (autumn species vs. adult hibernators) and the two modes of adult hibernation (in the field vs. under experimental conditions). Yet, we also observed taxon-specific differences in life-history strategies. For example, even though adult flight periods and basic life-cycle characters are very similar between *Allophytes oxyacanthae* and the various Central European *Agrochola* species, females of the latter genus lived distinctly longer, and also developed more than twice as many eggs. These differences are opposite to what one might expect from variation in body size (*Allophytes* is larger, with fore wing length 17–20 mm, compared to 14–19 mm in *Agrochola*; Skou 1991). In our experiments, *Allophytes oxyacanthae* laid three times larger eggs (mean diameter \pm 1 SD: 0.439 ± 0.079 mm, $n = 1249$) than *Agrochola circellaris* (0.133 ± 0.015 mm, $n = 235$; E. McMannis & K. Fiedler, pers. observ.). Hence, the overall investment in eggs was likely to be rather larger in *A. oxyacanthae* than among *Agrochola* moths. A possible explanation for the far higher egg number could be that early larval mortality is so high in *Agrochola* that a larger number of eggs are required to compensate for such losses. The mandatory tight matching between the timing of larval hatching and bud-break of host trees in spring could be important here.

In the adult hibernators *Conistra* and *Eupsilia* fecundity was overall far higher than in autumn moths. Differences in fecundity between these two genera were small in individuals kept over winter in the lab and only became distinct after hibernation in the wild. Eggs of *Conistra vaccinii* (0.279 ± 0.024 mm, $n = 664$) were considerably larger than in *Eupsilia transversa* (0.221 ± 0.029 mm, $n = 905$), which is the opposite pattern than with regard to body size (*Eupsilia transversa*: fore wing length 18.16 ± 0.64 mm, $n = 61$; *Conistra vaccinii*: 14.58 ± 0.53 mm, $n = 74$). These adult hibernators have much more time to develop eggs during their extended adult life span and, as shown above, they

indeed have the capacity to benefit from extra-nutrients obtained via fruit-feeding. High fecundity accompanied by small egg size indicates that they both are r-selected insects (see Davis et al. 2016), *Eupsilia* even more strongly so than *Conistra*. Larvae of *Eupsilia* and *Conistra* have a reputation to preying on insects like other spring caterpillars, including immatures of their own species (Schweitzer 1979; Pierce 1995; Ebert 1997–1998; see also Richardson et al. 2010). It may thus be desirable for a female to spread her offspring over many host plants, rather than laying multiple eggs at each site. As in *Agrochola*, a tight synchronization between larval hatching and budbreak is also of paramount importance in these adult-hibernating species. Hence, selection might have favoured investment into more, but smaller eggs in such species, if early larval mortality risks are particularly severe.

Methodological issues. Our data on life spans are underestimates of true potential physiological longevity, since we sampled moths from natural populations and hence their age and individual history at the onset of the experiment was unknown to us. However, this was true for all moths tested from all species and life-cycle types in the same manner. Moreover, we included date of capture as a co-variate to alleviate effects of pre-capture life-time as much as possible. Rearing all experimental insects from the egg stage under controlled conditions would of course have been optimal, but was out of scope for the present study due to the high demand regarding lab rearing. Overall, the high maximum longevity of all taxa observed (*Allophyes*: 22 d; *Agrochola* 69 d; *Conistra*: 198 d; *Eupsilia*: 159 d) indicates that laboratory conditions were suitable for the moth species concerned. An adult life span of close to 200 d may well represent a new record high for any temperate-zone noctuid moth that does not undergo a true diapause.

In the analyses presented above, we focussed on potential fecundity, i.e. the sum of eggs laid in captivity plus the mature oocytes remaining in a female's abdomen after its death. We feel this procedure to be justified since the mere number of eggs laid, viz. realized fecundity, can be misleading in experimental situations such as ours. For example, it was not always possible to offer high quality egg-laying substrates in such large amounts that females could have spread their eggs singly or in small groups, as they would do in nature. Hence, motivation to lay eggs may have been confounded by the circumstances applicable in captivity. Moreover, mating status and health of the moths may sometimes preclude that potential fecundity also translates into oviposition acts. However, analysis of realized fecundity yielded largely the same patterns as we present here with regard to potential fecundity (Zimmermann 2017).

In our experiments we offered banana as a standardized food. This is, of course, not a resource naturally available to any of our study species. We do not know whether decaying fruits that noctuid moths may encounter in autumn and winter in Central European woodlands, such as brambles, apples, plums or similar, may provide nutrients in different amounts than fresh banana slices. Hence, it remains to be seen if similar fecundity benefits might accrue in experiments employing more 'natural' food resources.

In summary, our experiments reveal that over a range of cold season moths, including two genera with unusually long adult life, there was no indication that facultative fruit-feeding, in comparison to nectar mimics, would enhance longevity. In contrast, beneficial effects on fecundity were pronounced in adult hibernators, which represent extreme cases of income breeders among the Lepidoptera. Autumn noctuid species, in contrast, turned out to be positioned more at the capital breeders' part of the continuum. It would be interesting to test if similar fecundity benefits can be found in other European moths that hibernate as adults. Among the Noctuidae, the genera *Lithophane* Hübner, 1821 and *Xylena* Ochsenheimer, 1816 are the most likely candidates to behave similarly as *Eupsilia* and *Conistra*.

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